Ågren, G.I. (ed.) 1984
State and Change of Forest Ecosystems -
Indicators in Current Research
Swed. Univ. Agric. Sci.
Dept Ecology & Environmental Research
Report nr 13, pp. 357-375.

NET PRIMARY PRODUCTIVITY AND MINERAL CYCLING IN THE MAIN FOREST TYPES AND TREE PLANTATIONS IN BELGIUM

PAUL DUVIGNEAUD AND SIMONE DENAEYER

Free University of Brussels. Faculty of Sciences. Department of Systematic and Ecology - 28, av. P. Heger, 1050 Brussels - Belgium

ABSTRACT

Concepts of ecosystem, biomass, mineralomass, energy flow, carbon cycle, productivity and mineral cycling are discussed in the first part of this report (Fig.2). The second part synthesizes the results obtained for NPP and mineral cycling in the main forest types and tree plantations studied in southern and central Belgium since 1965 under IBP followed by SCOPE. Climatic conditions are broadly the same but botanical composition, stand age, and soil conditions are different (Fig. 1, table 1).

NPP and annual nutrient absorption may vary widely and are not necessarily interrelated (Fig. 3). N,P,K and S absorption and storage in phytomass depend mainly on botanical composition of the stand (tabl. 2-3-4); the Ca and Mg mineral cycling dependsmore on soil condition (luxury consumption). N absorption and storage in Populus plantation is as high as in ecosystems associated with atmospheric N fixing microorganisms. The K and Ca annual absorption by the phytocoenosis may represent a great part of the available pool in the root layer in ecosystemsestablished on very acid soils (40 and 37%, respectively) and the storage of these nutrients in phytomass may be as high as in the root layer (table 3). Compared to the pool of total nutrients, the storage in phytomass is negligible for K, Ca and Mg, and corresponds to a small percentage of the N, P and S pool.

INTRODUCTION

In the ecosystem, the Carbon cycle (energy flow) is binded to the other cycles, not only to those of N, S and P, which, with C, form the principal organic matter of the living constituents, but also to those of several cations which, at diverse degrees (poly- or oligonutrients), are necessary for the development of plants, animals and microbes.

Under IBP, and then under SCOPE, we have participated to research programs, which have shown at national and international levels, the diversity of concepts, methods and techniques of the different teams, depending often on financial and tactical possibilities.

It is with changing possibilities that we have developped research programs at different levels between a minimum and a maximum program, as defined by ELLENBERG (1963) when creating the PT-IBP program. Our programs were concerned with numerous types of forest biogeocenoses, seminatural or planted, dispersed in central and southern Belgium (Fig. 1).

For the present paper, we choosed the most contrasted ones and also the most typical; map fig. 1 shows that those forests are dispersed on a small surface; nevertheless, the forests in the Ardennes endure a more continental climate.

Before tenting a review and synthesis of our results on belgian forests and plantations, it may be useful to define the concepts and terminology used by us in the field of biomass, primary productivity and mineral cycling.
Let us repeat that our researches place themselves between a maximum and a minimum program, between more or less analytical or synthetical considerations.

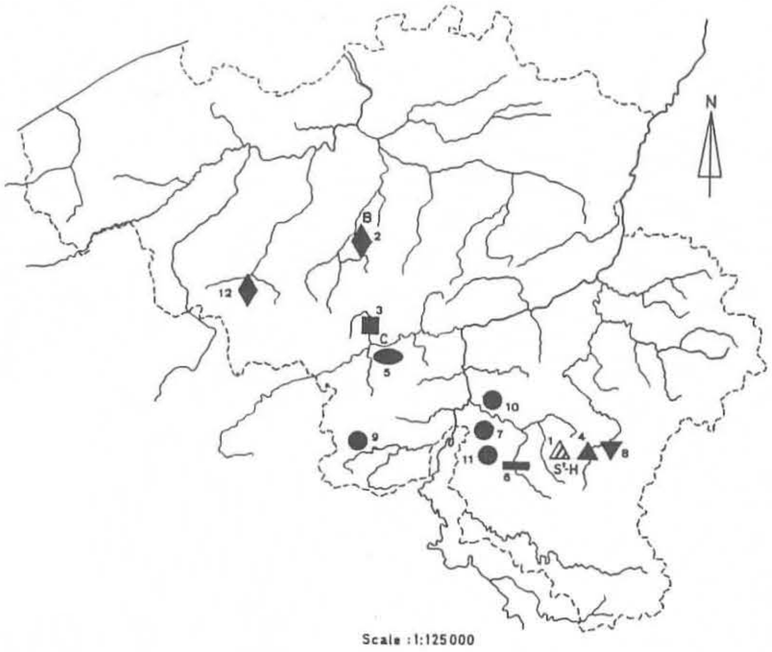

Fig. 1 - Localisation of the main forest ecosystems studied in Belgium (IBP and SCOPE programs).

1. Mirwart : Pseudotsuga menziesii plantation on acid brown earth; 2. Bruxelles : Populus cv. robusta plantation on loamy wet soil; 3. Charleroi : Betula pubescens plantation on colliery tip spoil; 4. Mirwart : Picea abies plantation on acid brown earth; 5. Charleroi : Robinia pseudacacia plantation on colliery tip spoil; 6. Daverdisse : Alneto-Coryletum on brown earth (island); 7. Houyet : Querceto-Coryletum on brown earth; 8. Mirwart : Fagetum on acid brown earth; 9. Virelles : Quercetum mixtum on calcareous soil; 10. Villers s.Lesse : Querceto-Crataegetum on pseudo-gley; 11. Vonèche : Querceto-Betuletum on podzolic soil; 12. Ath : Populus cv. robusta plantations 8-24-31 yr old, on silty-loamy soils.

Table 1. Main site characteristics, phytomass and net primary productivity of selected forests and tree plantations in southern and central Belgium.

SITE NUMBER/ECOSYSTEM *	1	2	3	4	5	6	7	8	9	10	11
Altitude	350	100	125	390	120	280	240	360	245	160	390
Mean annual temperature (°C)	7.5	9.5	9.4	7.5	9.4	8.2	8.1	7.5	8.0	8.1	7.4
Mean annual rainfall (mm)	1250	850	870	1250	870	1100	1050	1250	1050	1050	1300
Mean stand height (m)	36	25	10	19	10-12	9.7	24-4	31	20-13	20	22
Density (nb trees/ha)	217	204	5000	1065	475-850	32.930	163	156	260	192	63-359
Basal area (m^2.ha)	58.4	18.9	41.6	41.5	31.0	39.6	28.1	* 31.0	21.2	17.0	20.9
Age (yr)	70	20	14	55	25-18	15	117	144	75-35	90-20	135
pH Al	3.6	4.8	6.2	4.2	7.3	5.6	5.4	4.2	6.5	5.2	3.5
Phytomass (kg/ha)											
aerial parts											
tree layer boles+branches	396.0	87.4	73.5	184.5	85.5	98.7	256.6	370.7	114.7	149.6	198.7
leaves	7.7	4.8	3.2	16.1	4.6	2.5	3.5	3.3	3.5	3.1	3.2
herbaceous layer	0.9	1.1	1.7	0.2	0.7	1.3	0.7	0.5	2.2	1.4	2.3
total aerial parts	404.6	93.3	78.4	200.8	90.8	102.5	260.8	374.6	120.4	154.1	204.2
subterranean parts	67.4	11.6	22.7	70.1	17.0	19.7	55.4	75.2	35.3	32.1	38.9
Total Phytomass	472.0	104.9	101.1	270.9	107.8	122.2	316.2	449.7	155.6	186.2	243.1
Productivity (k. ha.yr)											
aerial parts											
tree layer boles+branches	20.1	15.0	9.4	10.5	7.3	9.8	7.9	7.2	6.3	5.1	3.1
leaves	2.7	5.1	4.0	2.8	5.2	2.5	4.2	4.1	3.9	3.5	3.6
herbaceous layer	0.8	1.1	1.5	0.2	0.7	1.3	0.6	0.5	0.7	1.4	1.8
total aerial parts	23.5	21.2	14.9	13.5	13.2	13.6	12.8	11.8	10.9	9.9	8.5
subterranean parts	4.1	2.0	2.8	4.1	2.8	2.0	2.3	2.2	2.3	2.4	1.6
Total Productivity	27.5	23.2	17.7	17.5	15.0	15.6	15.1	14.0	13.2	12.4	10.1

* Locality and botanical composition are given fig. 1.

1. Concepts (Fig. 2)

1.1. The ecosystem

The ecosystem is a functional system, incorporating a biocenosis to its environment. The basic ecosystemic unit is the biogeocenosis, composed of an homogenous biocenosis developped in an homogenous environment.
Ecologically linked, adjacent biogeocenoses, as those forming a lake, or a valley, or a catena of soils and vegetation, or a farm (agroecosystem) constitute more complex ecosystems, units of ecolandscapes or ecoregions.

In this paper, we shall use, as everybody does, the term "forest ecosystem" in its strictly limited biogeocenosis signification. We perfectly know that in true nature, a forest is generally a mosaïc or sequence of different forest biogeocenoses; this must never be forgotten in ecosystemic studies.

1.2. Biomasses and mineralomasses

The biocenosis is composed of a network of producers, consumers, decomposers, remineralizers joined by a flow of matter and energy initiated by the sun energy. This flow is constructive at the green plants producers level. It begins with the vegetation period, and, till the complete remineralisation of the elaborate materials, many years may pass. By convention, we have condensed the phenomena in one year, from the 1 January to the 31 December. So one may speak of annual energy flow, of annual nutrient cycling, as well as annual balance of phytomass or of nutrients (see later).

We call biomass B the mass of all the living organisms present in a surface unit (1 ha) of the biocenosis at the moment of observation; it may be expressed in kg or t, dry matter, kcal, kJ, a.s.o.

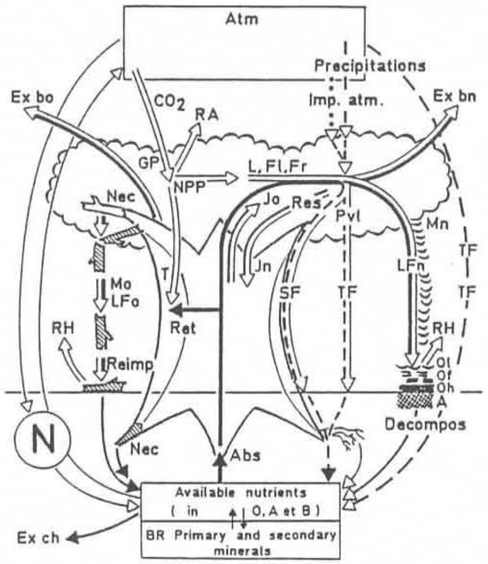

Fig. 2 – Schematic representation of biogeochemical cycles and balances in the forest ecosystem (for more explanation, see text).

We are more concerned by the phytomass B1, mass of the plant producers. In fact, phytomass contains organic matter and mineral substances (mineralomasses), which may be evaluated from the ash analysis. The "organomass" may be evaluated from the carbomass, but the problems of N, S, P are not clear.

Productivity is the rate of production of biomass; net primary productivity NPP is the rate of production of phytomass (by ha by year).

Following SOUKATCHEV, we consider the biocenosis environment as the biotope, divided in climatope, hydrotope and edaphotope.
In this paper, we principally put the accent on the available mineral nutrients offered to plants by the edaphotope.

1.3. Annual energy flow. Carbon cycle and balance.

At the producers level (green plants), the photosynthetic system (leaves in the canopy and ground layer) converts the solar energy (PAR, photosynthetically active radiation) in assimilates, made from CO_2 and H_2O.
This gross productivity of carbohydrates (GP) is first used for the maintenance respiration of the photosynthetic and nonphotosynthetic systems; what remains, netto assimilates production, is used for the construction of new tissues, organs and individuals; maintenance respiration and construction respiration form the autotroph's respiration RA.

what remains of GP and its transformation in new substances is thus

$$GP - RA = NPP$$

NPP, net primary productivity, divides in
- a contribution to the augmentation (increment) of the phytomass T1, principally wood, bark and seeds in deciduous forests, but also leaves in evergreen coniferous forests (see also resorption).
- a fraction which dies during the period (1 year) of observation : Mn (non predatory mortality) and falls in form of litter fall LFn of leaves, scales, inflorescences, roots, dead fruits, a.s.o.
- a fraction leached by the rain (pluvioleaching) Pvl and arriving to the soil in through fall and stem flow.
- a support to consumers C_2 (predatory mortality).
- an exportation Exbn of varied biological materials (pollen, current year twigs, leaves, resines, a.s.o.).

The index n is for new. It must be emphasized that annual energy flow starts only from leaves photosynthesis and does not incorporate organs or tissues (o for old) produced during previous years. Consideration for these will be taken in annual balances.

So, by a sommation method, it is possible to measure NPP

$$NPP = T_1 + LFn + Pvl + C_2 + Exb\ n$$

If we put down

$$LFn + Pvl + C_2 \equiv Eln \text{ (El for elimination)}$$

ans choose an area of forest without exportation by man (Exb n=0), we have,

$$NPP = T_1 + Eln$$

Theoretically, the litter fall LFn superposes itself to the preexisting litter L ; a part of LFn may be added to F if the decomposition is slow.
An other part of LFn may be transformed into humus; the quantity of new humus δHn will be added to the preexisting humus H.
For simplification, we call humus H all kind of black organic matter

resulting from the transformation of L; still an other part may be remineralised.

We may call NBP, net biocenosis productivity, the sum of organic matter living or dead, produced by the energy flow

$$NBP = T + \delta Ln + \delta Hn$$

T is thus the living matter added to the initial biomass; but opposed to this, a fraction of the initial biomass dies (Mo) forming a certain quantity of standing dead wood (necromass, Nec), which falls little by little under the influence of gravity, wind, birds, a.s.o.
Every year, a litter fall of old dead wood and old leaves in the case of evergreen forest may be collected, forming LFo; a mean LFo, established on measurements made on successive years, may be assimilated to the wood (and leaves) dead in mean year.

$$\text{So, } LFo \simeq Mo$$

LFo is also a reimportation of organic matter in the system, a second source of carbon for a second decomposers trophic chain.

If we establish the balance between the living matter added to the initial biomass during observation time and the matter lost by death by this initial biomass during the same period, we have

$$\Delta B = T - Mo$$

which is the true increment of russian ecologists, the dialectic interpenetration of life and death.

Like LFn, LFo is progressively decomposed, humidified and remineralized. After 1 year, it remains

$$\delta Lo + \delta Ho$$

If we put down $\delta Ln + \delta Lo = \Delta L$

and $\delta Hn + \delta Ho = \Delta H$

We have finally

$$NEP = \Delta B + \Delta L + \Delta H$$

NEP being the net ecosystem productivity, which, contrarily to NPP and NBP, results from a balance, and not from a flow of energy.

Sometimes, the reimportation of autochtonous materials is accompanied by the importation of allochtonous materials; this phenomenon, very important in rivers and lakes, where the first living step in energy flow is bacteriosynthesis (replacing photosynthesis) is unimportant in forests, at the exception of urban and industrial zones.

Things are still more complicated because, in the spring takes place a remobilisation Jo of certain assimilates stocked the previous year in old parts of the phytocenose, which are translocated towards the newly formating organisms, principaly leaves L; this remobilisation must be substracted from NPP; at the end of the growing season, the inverse phenomenon happens : organic substances are put into reserve in old parts for next year; this resorption Jn must be added to NPP.
If we admit that $Jn \simeq Jo$, the phenomenon is not important in the estimation of NPP.

The importance of this internal resorption pool and cycle is elsewhere, principaly in the functionning of the N and P cycles (see later).

If L = the weight of leaves at the end of the growing period, the resorption is in a deciduous forest

$$Res = L - LLF - PVL = Jn$$

(LLF for leave litter fall).

1.4. Biological cycles and geochemical flows

a.- In their annual flow through the phytocenosis, the assimilates (Carbon flow) are combined with mineral elements (principally nutrients), from which a part is stocked in the annual increment (retention Ret), an other part is recycled in litter fall and leaching (restitution Rest n), an other part is lost by exportation of biological products Exb n. Note n for newly produced organs. This is called biological cycle :

$$Abs = Ret + Rest\ n + Exb\ n, \text{ with}$$

$$Rest\ n = LF\ n + Pvl$$

(In Rest n must be included restitution by root litter and root exsudates.
Technically, this is generally quite impossible to realise) is not really an annual one. The elements retained in wood and bark are stocked for a long period; they are released progressively by the dead wood fall (LFo).
As for carbon flow, they may be included in an annual nutrient balance

$$\Delta \text{ mineralomass} = \text{Retention} - \text{Reimportation}$$
$$\text{Accumulation} = \Delta min = Ret - LFo$$

This is theoretical. One may also consider a total annual restitution, adding LFo to LFn in LFt (total litter fall).
The elements contained in LFn may take a long time to be remineralized; the turn over rate :

$$\theta = \frac{LF}{L + H}$$

varies following the type of humus.

b.- The biological cycle is completed by a geochemical flow, characterized by
- importation from atmospheric precipitations (liquid, solid and gazeous?), Imp.atm.
- importation from dissolution or decomposition of bed rock or secondary minerals in soil, Imp.s.
- exportation by run off, erosion, percolation through soil, Ex.ch.

The expression of this flow is the balance

$$Imp.atm. + Imp.s. - Exp.ch.$$

Let us remark here that pluvioleaching, which may be estimated by the difference between the composition of precipitations under forest and atmospheric precipitation, is thus :

$$Pvl = TF + SF - Imp.atm.$$

c.- Nitrogen, which may be fixed biologically from the atmosphere, or biologically liberated to the atmosphere by denitrification or NH_3 volatilisation, may be considered as forming a special biological cycle.

d.- Sometimes, as it is generally so in agriculture, man compenses exportation losses by importation of fertilizers.
This "anthropic cycle" is specially important in the so actual problem of whole tree exploitation for biomass.

e.- Extremely important is the problem of the soil reserve in available nutrients. The available nutrients (in soil horizons O,A and B, eventually C) are in instable equilibrium with those in the bed rock, or primary or secondary minerals.
But which is the good definition for availability?
Often, exchangeability is considered. But the possibilities of roots are greater as generally throught about. So, the law of forest perpetuation of HARTMANN must be considered.

1.5. The resorption cycle

Discretely develops the internal remobilisation-resorption cycle. In this important conservative mecanism, nutrients are not exposed to remineralisation or lost by run off , drainage or erosion. RYAN and BORMANN have shown that, even if the nutrient pool (mineralomass) is eliminated by clear cutting, the resorption cycle is quickly reestablished in the young regenerating phytogeocenosis. The most important nutrients engaged in the resorption cycle are N and P.

1.6. In conclusion, the annual absorption defines the intensity of mineral cycling, the sobriety degree of the system, the fertility of the soil.
The knowledge of mineralomass of different compartments permits the evaluation of losses by thinning or cutting. Of course, those data must be related to the mineral reserves of the soil; the available fraction of those reserves must be evaluated, but our knowledges about this problem are still vague.

2. Comparison of net primary productivity and mineral cycling

2.1. Methodology

Phytomass and net primary productivity are established by direct measurements on representative trees (3 to 6) cut down, after inventory of the forest stand based on DBH 1.30 m (following IBP recommendation). Boles, branches and twigs are cut up in diameter and age categories. Phytomass and NPP of the phytocoenosis are calculated using allometric relationships. The phytomass of the roots is evaluated on the base of an average value of the ration aerial/subterranean plant parts given by several workers; NPP is based on the ratio phytomass NPP of the aerial parts. Phytomass and NPP of the ground layer are measured by harvesting the aerial parts of a given area (1 to 4 m^2) and collecting the underground part in the root layer of a smaller area (50 x 50 cm for ex). The annual litterfall is measured in litter traps (IBP recommendation). More informations on phytomass and NPP measurements are given in DUVIGNEAUD et al. (1971) and DUVIGNEAUD and KESTEMONT Ed. (1977). As in many other NPP and mineral cycling studies, root litter has not be measured because technical difficulties.

The annual nutrient absorption is estimated on the base of a simplified concept proposed by OVINGTON (1968) and followed by many workers : absorption = retention + restitution = nutrients retained in annual increment of wood and bark (dry weight x nutrient content); nutrients released by annual litterfall (dry weight of dead leaves, current twigs, etc. x nutrient content) and by rainleaching, which is very important for K. If rainleaching is not measured, the annual restitution of K has to be calculated on the base of the K content of green leaves. Nutrient storage in phytomass (mineralomass) is obtained by multiplying the dry weight of boles, branches (bark and wood separetely because high differences in nutrient content), twigs, leaves etc. by nutrient content.

The nutrient pools of the soil are evaluated by multiplying the nutrient content (exchangeable and total form) by the weight of the air-dried soil ($\leq$ 2 mm) corresponding to the depth of the root layer. In order to make comparison of soils without taking into account the root layer depth, the nutrient pools are also calculated for a given soil weight.

2.2. Net primary productivity and annual nutrient absorption
(Fig. 3, tabl. 1 and 2)

Remark : Because of the lack of accuracy in measurement of net primary productivity of subterranean plant parts, only aerial NPP has been considered in this comparative study.

Table 2 - Annual nutrient absorption in selected forests and tree plantations in Belgium.

Site Number	Ecosystem	NPP (*) aerial+ subterr	kg.ha.yr					
			K	Ca	Mg	N	S	P
1	Pseudotsugetum	27.6	36	50	8	85	20	8
2	Populetum	23.1	182	286	33	235	70	34
3	Betuletum	17.7	102	125	34	131	28	16
4	Piceetum	17.6	58	76	14	96	16	8
5	Robinietum	16.0	196	159	35	303	43	33
6	Alneto-Coryletum	15.6	58	103	19	173	21	11
7	Querceto-Coryletum	15.1	115	172	23	129	17	12
8	Fagetum	14.0	51	75	8	93	10	8
9	Quercetum mixtum	13.2	69	201	19	91	13	7
10	Querceto-Crataegetum	12.4	82	90	27	98	19.	6
11	Querceto-Betuletum	10.1	73	60	17	115	12	9

* t.ha.yr

NPP varies widely with botanical composition, stand age and soil condition. The highest values are found in introduced species plantations : 27.5 t.ha.yr in a 70yr old *Pseudotsuga menziesii* plantation and 23.5 t.ha.yr in a 20 yr old *Populus* cv. *robusta* plantation. High NPP values have also been found in tree plantations on colliery tip spoils: 18 and 16 t.ha.yr in a 14 yr old *Betula pubescens* and in a 18-25 yr old *Robinia pseudacacia* plantation, respectively. Those values are higher than in our best native hardwood forests (13 t.ha.yr max.).

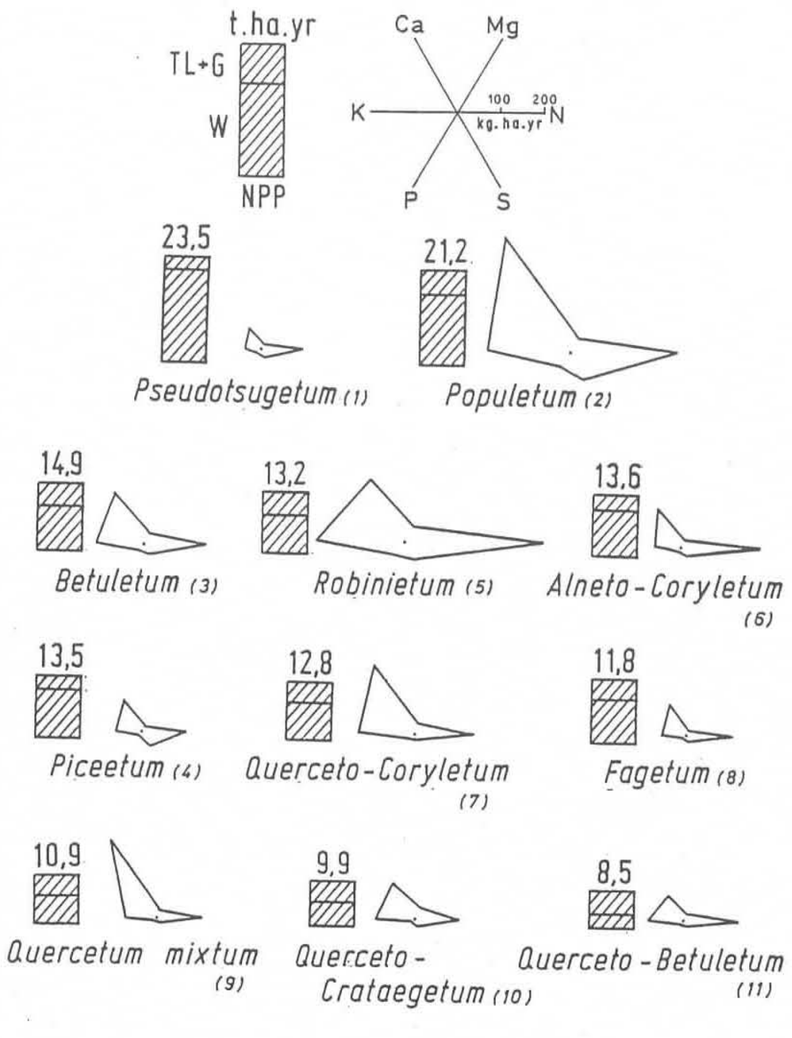

Fig. 3 - Comparison of NPP and annual nutrient absorption in selected forests and tree plantations in Belgium.
NPP = net primary productivity (aerial parts only); TL = tree leaves; G = ground layer; W = wood increment. In ( ), site number (for more information, see table 1).

The NPP differences are still more significant if only wood production is considered : 20 and 15 t.ha.yr in Pseudotsuga and Populus plantations respectively, 6-8 t.ha.yr in hardwood growing under good or normal soil condition, and as low as 3 t.ha.yr in very bad soils.

Annual nutrient uptake (fig. 3, table 2) on poor and acid soils is always low, even when the NPP of the ecosystem is high, for ex. in the beech and in the coniferous plantations. The most productive among them, the Pseudotsuga plantation, is charaterized by a very low nutrient uptake; an other high productive ecosystem, the Populus plantation contrasts strongly with the Pseudotsuga plantation because its nutrient uptake is very high; the soil nutrient status in the former system is also much higher (see later, table 3, 5a and 5b). Although the NPP of our good oakforests is not higher than for the studied beechforest (on acid soil), their nutrient absorption is always higher.

K absorption depends mainly on the botanical composition (Populus and Robinia are the most K "consuming" species, Pseudotsuga and Picea, the lowest), whereas Ca and Mg absorption are closely related to the status of those nutrients in the soil (luxury consumption, accumulation in bark, etc.).
The annual K absorption by the phytocoenosis is also influenced by the phytomass of ground layer, because herbaceous plants are always high K consuming species (see also point 2.5).

The highest values for N absorption are found in the Populus plantation and in ecosystems associated with N fixing microorganisms : Robinietum, Alneto-Coryletum; in other native hardwood forests and in the coniferous plantations, N annual absorption is much lower and does not vary widely with botanical composition or soil condition.

The same may be said for P : the annual absorption is much higher in introduced broadleaved plantations (Populus, Robinia) than in hardwood forests or coniferous plantations, even when their NPP is high (for ex : Pseudotsuga).

S annual absorption seems more affected by environmental conditions. In normal soil and air conditions, the absorption of S ranges between 12-20 kg S.ha.yr (table 2). Much higher values (43-70 kg.ha.yr) are found in ecosystems located in urban and industrial areas : Robinia and Populus plantations. Probably, the high S content of the soil derived from colliery tip spoil and perhaps atmospheric pollution by SO_2 (iron and steel industry, house heating) are responsible of this high S absorption by the phytocoenosis.

For the adjacent beech forest and spruce plantation, throufall and stemflow have been analyzed for their sulphate content.
If the S amount leached by rain is added to the S amount returned by litterfall in the calculation of annual absorption (see point 2.1), high values for annual S absorption may also be obtained for ecosystems far away from urban or industrial activities (till 50 kg S.ha.yr for the Picea plantation).
But, as suggested recently by a number of authors, sulphate impaction, filtering action of forest ecosystems and rain-washing are probably responsible of the high sulphate content of throughfall (MAYER and ULRICH 1974, DENAEYER and DUVIGNEAUD 1977, LIKENS et al. 1977).

Table 3 - Nutrient storage in standing crop (aerial parts) and in soil in various forest types and tree plantations in Belgium; "total" form in t and exchangeable form in (kg).

Site number	ECOSYSTEM	Depth root layer (cm)	Soil weight (t)	Phyto-mass aerial parts (t)	by hectare											
					N		S		P		K		Ca		Mg	
					Phyto mass (kg)	Soil (t)	Phyto mass (kg)	Soil (t)	Phyto mass (kg)	Soil (t)	Phyto mass (kg)	Soil t-(kg)	Phyto mass (kg)	Soil t-(kg)	Phyto mass (kg)	Soil t-(kg)
1	Pseudotsuga menziesii plantation	56	4425	405	654	6.4	206	1.5	54	1.3	200	- (194)	245	- (340)	48	- (90)
2	Populus cv. robusta plantation	60	7000	101	666	9.5	139	1.9	80	5.2	323	- (770)	423	- (18460)	59	- (2380)
3	Betula pubescens plantation	50	8000	73	229	36.8	43	7.1	28	12.0	128	16 (1840)	170	16 (14400)	36	48 (2496)
4	Picea abies plantation	60	4229	201	434	5.7	127	4.2	27	1.3	179	64 (159)	225	4 (186)	39	11 (83)
5	Robinia pseudacacia plantation	50	8000	93	733	60.7	127	9.7	71	3.6	283	- (814)	540	- (26400)	66	- (1586)
6	Alneto-Coryletum	50	6790	100	519	7.7	51	-	30	-	113	76 (207)	220	10 (1390)	30	23 (202)
7	Querceto-Coryletum	55	7250	261	712	6.4	107	-	52	4.5	403	177 (771)	1619	37 (5900)	57	80 (1003)
8	Fagetum	55	8850	375	953	23.3	96	2.7	73	6.2	412	165 (596)	668	8 (1042)	115	59 (186)
9	Quercetum mixtum	50	1360	121	406	4.5	51	-	52	0.7	245	27 (157)	868	133 (13600)	81	6 (151)
10	Querceto-Crataegetum	60	7760	154	481	8.7	100	-	37	3.3	316	249 (802)	495	28 (2462)	61	47 (2418)
11	Querceto-Betuletum	90	10900	205	593	8.2	70	-	44	1.6	226	181 (333)	395	39 (128)	46	18 (214)

2.3. Nutrient storage in phytomass

The mineralomass is not necessarily related to the phytomass because as well as for nutrient absorption, nutrient storage is greatly influenced by botanical composition and soil condition (table 3); this feature appears still more if comparison of mineralomass values is made on a same weight basis (100 t wood phytomass, for ex, see table 4). Mineralomass in coniferous plantations is always lower than in hardwood forests : the highest values were found in Populus and Robinia plantation, which, as seen previously, require large amounts of nutrients. Ca mineralomass is the most variable because of soil influence (maximum on calcareous soils) and of accumulation in the bark (especially in oakforests).

The highest values for N storage in phytomass were found in ecosystems associated with N fixing microorganisms (Robinietum and Alneto-Coryletum) and in Populus plantations; N storage in the different types of hardwood forests is nearly the same.

P storage in phytomass is very specific : very low (7-12 kg/100 t) in coniferous plantations, average in hardwood forests (15-20 kg) and very high in Populus and Robinia plantations (66-55 kg, respectively).

These two ecosystems, characterized by a very high N-P-K storage in their phytocoenosis, have also the highest S mineralomass; this fact reflects probably and at the same time, the high requirement of these two species and the environmental conditions (atmospheric SO_2 pollution and high S content of the soil).

Table 4 - Comparison of mineralomass of selected forests and tree plantations in Belgium

Site number	Ecosystem	kg/100 t wood phytomass					
		K	Ca	Mg	N	S	P
1	Pseudotsugetum	43	52	9	137	47	12
2	Populetum	183	354	42	512	109	66
3	Betuletum	111	227	43	271	58	31
4	Piceetum	66	73	14	119	52	7
5	Robinietum	214	504	52	667	113	55
6	Alneto-Coryletum	108	293	34	471	43	26
7	Querceto-Coryletum	129	522	19	235	38	16
8	Fagetum	100	169	29	229	24	17
9	Quercetum mixtum	142	675	63	256	33	20
10	Querceto-Crataegetum	171	309	36	260	61	19
11	Querceto-Betuletum	79	184	18	237	29	14

2.4. Relationships between annual absorption, storage in phytomass and nutrient pools in the soil

Total amounts of exchangeable cations and total N,S,P,K,Ca and Mg contained in the root layer of each ecosystems are given table 3; a comparison for the eleven ecosystems is made on a same weight basis (5000 t soil.ha, as a mean value for a mean rooting depth) in table 5a - 5b. The lowest values for exchangeable cations are always found in acid soils; the Ca^{++} pool is the most variable one, because wide variation in chemical composition of the bedrock in the various ecosystems; the more stable K^+ pool may be very high in special soils (colliery tip spoil).
The pool of exchangeable cations represents only a small fraction of the "total" form, especially for K, which is often the most abundant nutrient, if total form only is considered. The N pool (4-16 t . 5000 t soil in normal conditions) is especially high in ecosystem associated with N fixing micro-organisms (38 t . 5000 t soil in Robinia plantation).

Compared with nutrient pools in the soil, annual nutrient uptake by vegetation corresponds to 10-40% of the exchangeable K pool (maximum on calcareous soils), 1-37% from the exchangeable Ca pool (max. on very acid soils) and 1-17% of the exchangeable Mg pool (max. on very acid soils).
The total amount of K stored in the phytomass is always very high and represents from 50% to 100% of the K^+ pool and even more than 100% when the soil is very acid. The same may occur for Ca (20% in normal soil condition) and to a lesser extend, for Mg (from 5 to 50% if the soil is very acid).
Compared with the pools of total K-Ca-Mg in the soil, storage in the phytomass is negligible (a few percent).
Compared to the total amounts of N, S and P in the root layer of the ecosystems, the annual absorption by the phytocoenosis represents only 0.3 - 2% for N, 1-4 % for S and less than 1% for P; the storage of these nutrients in phytomass represents less than 10% of their absolute amounts in the root layer.

Table5a - Comparison of nutrients pools in the soil of 11 selected forests and tree plantations (*) in Belgium.

	kg of nutrients (exchangeable form) for 5000 t soil/ha										
Site number	1	2	3	4	5	6	7	8	9	10	11
K	219	547	2375	188	510	153	630	337	575	515	150
Ca	384	13234	18000	220	16315	1024	4075	589	(50000)	1585	60
Mg	102	1690	1560	98	930	202	690	105	555	1560	100

* localisation and main characteristics are given fig. 1 and table 1.

Table 5b - Comparison of nutrient pools in the soil of selected forests and tree plantations in Belgium

Site number	Ecosystem	t of nutrients (total form) in 5000t soil/ha					
		K	Ca	Mg	N	S	P
1	Pseudotsugetum	-	-	-	7	1.7	1.5
2	Populetum	-	-	-	7	1.3	3.7
3	Betuletum	10	10	30	23	4.4	7.4
4	Piceetum	76	5	13	6	4.9	1.5
5	Robinietum	-	-	-	38	6.0	2.3
6	Alneto-Coryletum	56	7	23	4	-	-
7	Querceto-Coryletum	122	26	55	4	-	3.1
8	Fagetum	93	5	33	13	1.5	3.5
9	Quercetum mixtum	98	490	24	16	-	2.7
10	Querceto-Crataegetum	160	19	30	6	-	2.1
11	Querceto-Betuletum	83	19	8	4	-	1.7

2.5. Influence of age on nutrient uptake and storage in phytomass

Table 6 and fig. 4 summarize a comparison made between three Populus plantations 8 - 24 and 31 yr old.

Annual absorption increases with stand age except for K. This nutrient is dominant in the 8 year old plantation, because the net primary productivity of ground layer (K consuming species) is much higher than the NPP of the young trees. Ca is the dominant nutrient in the 31 yr old plantation because the tree NPP has become very high and because the nutrient accumulates in the bark of boles and branches.

Nutrient recylcing is very high (85-90%) in the 8 yr old stand, because high NPP and nutrient absorption, and total decay of the groundlayer.

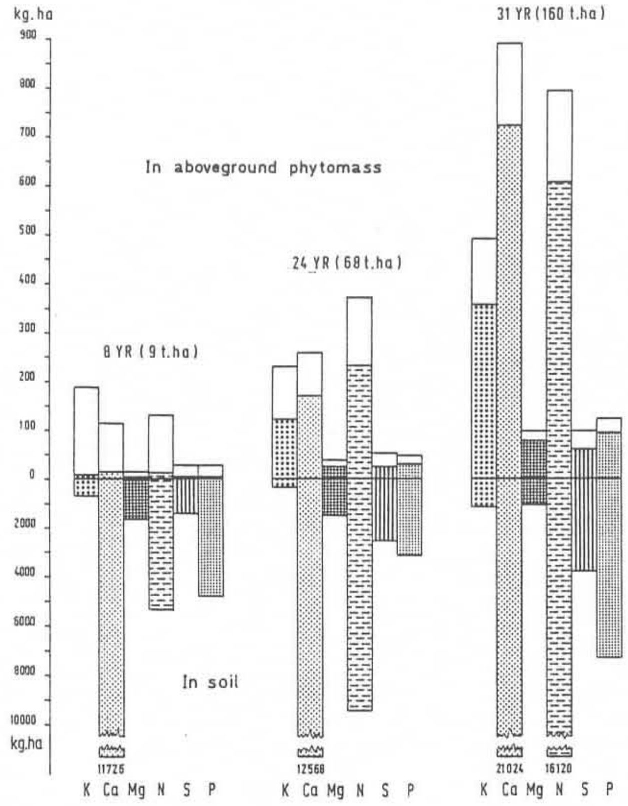

Fig. 4 - Distribution of nutrients in phytomass and in soil (root layer) in three Populus cv. robusta plantations of various age located near Ath (Central Belgium). White : in tree leaves and ground layer; grey : in bark and wood; in ( ) : phytomass. For K,Ca,Mg in the soil : exchangeable form; for N,S,P, total form.

Table 6 - Comparison of annual nutrient absorption (n.a) in three Poplar plantations (near Ath, in Belgium) of different ages.
R = nutrients retained in wood increment; r = nutrients released by Litterfall; P : Populus; C = coppice (Sambucus nigra); GL = ground layer; T = total.

Age yr	NPP t.ha.yr aer.+subt		kg.ha.yr					
			K	Ca	Mg	N	S	P
8	P 1.8 C 0.4	R	12	12	2	18	3	3
	GL 6.1 T 8.3	r	185	108	12	122	24	23
		n.a.	197	120	14	140	27	26
24	P 12.4 C 4.1	R	40	52	8	77	8	11
	GL 1.7 T 18.2	r	102	124	16	115	25	13
		n.a.	142	176	24	192	33	24
31	P 26.3 C 2.1	R	84	165	17	153	15	29
	GL 2.0 T 30.4	r	135	198	22	153	38	17
		n.a.	219	363	39	306	53	46

With increasing NPP of perennial tissues, nutrient recycling decreases (50 - 60%) and nutrient storage increases; K, Ca and N storage is especially high in the 31 yr old stand. Compared with the exchangeable K pool in the root layer, K storage in phytomass becomes very high (from 27 to 72% with increasing age); the mineralomass of the other nutrients represents only a small percentage of the soil pool (fig. 4).

Compared to the N pool of the other studied ecosystems, the N pool of mature Populus plantations seems very high; although not so charateristic, the same may be true for P. Perhaps, the high content of these nutrients in litterfall, especially of ground layer (Sambucus nigra, Urtica dioica are the dominant sp.) may contribute to the increase of N and P pools in the soil.

CONCLUSION

The comparison of eleven different forests and tree plantations growing under similar climatic conditions shows that :

1. Net primary productivity depends more on the botanical composition of the ecosystem than on soil condition and nutrient absorption.

2. Introduced species (Pseudotsuga menziesii, Picea excela, Populus cv. robusta, Robinia pseudacacia) are more productive than native species (Quercus robur, Q. petraea, F. sylvatica).

3. The highest NPP is not necessarely linked with the highest nutrient absorption (fig. 3) : the very low value found for the Pseudotsuga plantation (NPP : 23.5 t.ha.yr) contrasts strongly with the very high nutrient absorption of Populus plantation (NPP : 21.2 t.ha.yr).

4. The annual absorption of Ca and Mg depends mainly on soil condition (luxury consumptions) while N, P, K and S absorption is more specific : Populus and Robinia plantations are the most 'consuming" ecosystems coniferous plantations, the lowest (table 2).

5. The same general trends characterize the storage of nutrients (mineralomass) in the phytomass (table 3-4) : the storage of N, P, K and S is especially high in Robinia and Populus plantations; it should be observed that the N storage in the Populus plantation is as high as in the Robinia plantation, associated with the atmospheric N fixing Rhizobium.
It is obvious that the export of nutrients by clearcutting shall be much higher for a Populus plantation than for a Pseudotsuga plantation.

6. The annual nutrient absorption by the phytocoenosis represents only a small percentage of the exchangeable nutrient pool in the root layer of good soils, but represents 17 - 37 and 40% for Mg, Ca and K respectively in poor and acid soils.

   In such conditions, the total amounts of K stored in the phytomass may be as high (and even higher) than in the soil root layer (table 3). But is exchangeable K really significant or not, that is the question.

   Compared to the pool of "total" K, Ca and Mg in the root layer, the mineralomass of these nutrients is negligible. Compared to the pools of total N, P and S in the soil, the nutrient stored in the phytomass represent less than 10%.

7. Although provisional because several datas are failing (for ex., amounts of nutrients released by root exsudate and root litter, by dead wood fall, etc.) this comparative study of eleven forest ecosystems located in a very small area emphazises the diversity of the interelationships net primary productivity/mineral cycling, and the complexity of the plant/soil relations.

REFERENCES

Duvigneaud, P. et Froment, A. 1969. Eléments biogènes de l'édaphotope et phytocénose forestière. - Bull. I.R.S.N. Belg. 45, 25 : 1-48.

Duvigneaud, P. Denaeyer, S. et al., 1971. Recherches sur l'écosystème forêt. - Mémoire n° 164 - I.R.S.N., Bruxelles, 101p.

Duvigneaud, P. and Denaeyer, S., 1975. Mineral cycling in Terrestrial Ecosystems. In : Productivity of World Ecosystem. Nat. Acad. Sc. Washington D.C., pp 133-154.

Likens, G.E. et al., 1977. Biogeochemistry of a forested ecosystem. - Springer N-Y - Heidelberg - Berlin, 146p.

Mayer, B. and Ulrich, B., 1974. Conclusions on the filtering action of forests from ecosystem analysis. - Oceol. Plant. 9, 2 : 157-168.

In : Productivité biologique en Belgique. - Duvigneaud, P. et Kestemont, P., Ed., SCOPE 1977, Duculot, Paris-Gembloux.

- Duvigneaud, P. et al. La hêtraie ardennaise à Festuca altissima à Mirwart. Biomasse et productivité primaire. pp. 107-154.
- Kestemont, P. et al. Biomasse et productivité primaire d'une pessière à Mirwart. pp. 161-176.
- Kestemont, P. Biomasse et productivité primaire de la douglasière à Mirwart. Plantation de Pseudotsuga menziesii. pp. 177-189.
- Denaeyer, S. et Duvigneaud, P. Cycles biogéochimiques dans une hêtraie et une pessière à Mirwart. pp. 301-311.
- Duvigneaud, P., Denaeyer, S. et Kestemont, P. Productivité de forêts belges de types variés. pp. 489-500.

in : Ecosystème, cycle du carbone, cartographie.
Duvigneaud, P., Denaeyer, S. et Brichard, C., Ed. SCOPE 1980, Minist. Ed. Nat. et Cult.

- Duvigneaud, P. et al. Une biogéocénose "Plantation de Populus" dans l'écosystème bruxellois. pp. 54-90.
- Duvigneaud, P. et al. Des terrils de charbonnage considérés comme écosystèmes. pp. 199-250.

Ryan, D.F. and Bormann, F.H., 1982. Nutrient resorption in Northern Hardwood Forests. Bioscience, 32, 1 : 29-31.

Presented at the ESF Workshop "What properties of a forest ecosystem give the best information on state and change", March 21-24, 1983, Uppsala, Sweden.